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THE WINGS OF INSECTS.

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CHAPTER IV.

The Specialization of Wings by Addition.

I. THE DEVELOPMENT OF ACCESSORY VEINS.

THE more important of the generalizations reached in the course of the present investigation are two in number; first, the recognition of certain features of the venation of the wings of insects, which occur in the more generalized forms of a large proportion of the orders of this class, has enabled us to present a hypothetical type to which the wings of all orders may be referred;[1] second, if we leave out of consideration the anal area, that portion of the wing traversed by the anal veins, we will find that in nearly every case each order of insects is characterized by either a reduction or a multiplication of the wing-veins; in certain orders the tendency is in one direction, while in others it is in the opposite; but either of these tendencies may be correlated with a similar tendency in the anal area or with the opposite one.

In the preceding chapter we pointed out the various ways in which the number of the wing-veins in the preanal area is reduced. In nearly every case we found the reduction of the preanal area accompanied by a similar tendency in the anal area, or, if a reduction had not taken place, there was no increase in the number of veins of this area, the tendency being towards the production of a few-veined wing. The Trichoptera, however, form an exception to this rule.

We have now to consider several types of wings, in each of which there is taking place an increase in the number of veins of the preanal area, the tendency being towards the formation of a many-veined wing. In speaking of an increase in the number of veins, reference is made only to a multiplication of the branches of the principal veins. In no case is there an increase in the number of principal veins. And this increase in the number of branches may be confined to one or two of the principal veins, while the number of the branches of some of the other veins may be reduced, the expanding of some parts of the preanal area resulting in a crowding of other parts. In some cases we will find that the multiplication of wing-veins extends to the anal area also ; in others we will find the anal area greatly reduced. But even in those cases where the anal area is reduced, the total result has been the production of a many-veined wing.

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[1] *American Naturalist*, vol. xxxii (February, 1898), pp. 81–89.

In the many-veined wings both the longitudinal veins and the cross-veins are increased in number. In most cases where there are many cross-veins it is impracticable to distinguish from others those particular cross-veins to which we applied special names in describing the few-veined wings.[1] But in the case of the longitudinal veins it is necessary to distinguish the primitive veins, that is, those of our hypothetical type, from the veins that have been developed in addition to these. For if this is not done it will be impossible to point out the changes that have taken place in the course of the development of each of the various types of many-veined wings. We therefore apply the term accessory veins to these secondarily developed longitudinal veins, and retain the same nomenclature for the primitive veins that we used in describing the few-veined wings.

Accessory veins may be borne by any of the primitive longitudinal veins ; and they may arise from either of the two sides of such a vein. In most cases it is unnecessary to designate the individual accessory veins, as, usually, it will be sufficient for descriptive purposes to indicate the number of these veins that have been developed upon a particular longitudinal vein. In fact, in certain cases more than this could not well be done owing to the irregularity of the veins. On the other hand, in many cases the accessory veins borne by a single primitive vein present a high degree of regularity, and it is evident that they have been developed in a regular sequence. Under these circumstances it is practicable to designate them individually; and we have devised the following method for this purpose.

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[1] *American Naturalist*, vol. xxxii (April, 1898), pp. 233, 234.

The accessory veins arising from one side of a single primitive vein are considered as a single set, and to each set of veins a distinct set of numbers is applied, beginning with the oldest (*i.e.*, the first-developed) member of the set.

By this method homologous veins, when a homology exists, will bear the same number. But it should be remembered that as accessory veins have arisen independently in many different groups of insects, it often happens that accessory veins similar in position, and bearing the same number in our system, are merely analogous and not homologous.

In order to apply this system it is necessary to know, in the case of each group of insects studied, the sequence in which the members of the particular set of veins under consideration have been developed. For additions to such a set of veins may be made to the distal end of the series, or to the proximal end, or may be interpolated at some distance from either end.

Frequently an examination of the wing of an adult insect is sufficient to determine this sequence. But the determination can be made in a much more satisfactory manner by a study of the tracheation of the wings of the nymph or pupa. For in the many-veined insects the longitudinal veins, both primitive and accessory, are developed about tracheæ; and it is much easier to determine the homologies of the tracheæ of an immature wing than it is to determine the homologies of the wing-veins of the adult. And, too, in this way we are able to eliminate the cross-veins which are not preceded by tracheæ in the forms used for illustration here. We will, therefore, use for this purpose the wings of immature insects.

Accessory veins added distally. — If the radial tracheæ of the pupa of Chauliodes (Fig. 53) and of the pupa of *Corydalis cornuta* (Fig. 54) be examined, it will be seen that both differ from our hypothetical type in the presence of a greater number of branches of the radial sector. And a comparison of the two figures shows that the increase in the case of Corydalis has been greater than in the case of Chauliodes. Farther, the presence of fine twigs at the tip of the trachea R_5 indicates the method of increase, which is doubtless as follows : the branches have been added one after another to the tip of trachea R_2, there being a migration of the base of each accessory trachea towards the base of the wing, thus making room for the addition of new branches. In this case the first accessory vein is the proximal one.

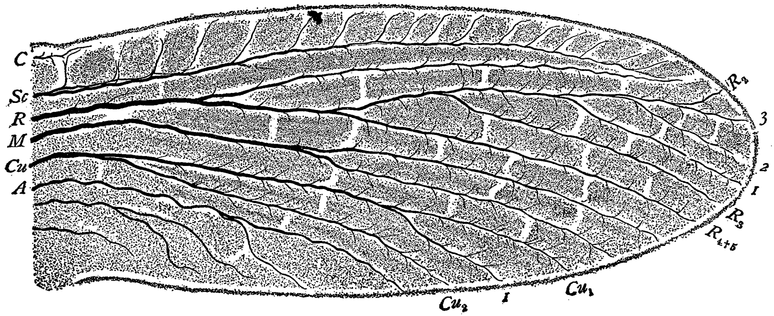

FIG. 53. — Wing of a pupa of Chauliodes.

In Sialis (Fig. 55) the accessory veins have been developed in a similar way, but they are on vein R_3 and on the cephalic side of this vein. Here, too, the first accessory vein is the proximal one. But it should be noted that the numbers of the veins increase in the opposite direction from what they do when the accessory veins are added distally on the caudal side of a primitive vein, as in the radial sector of Chauliodes and Corydalis.

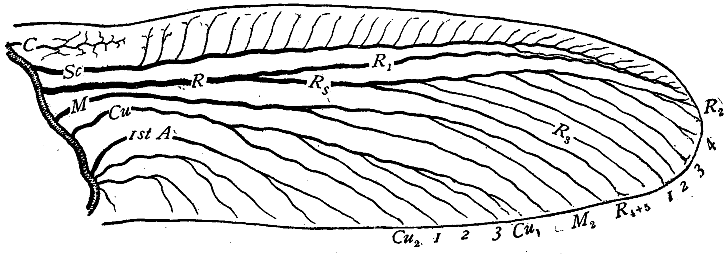

FIG. 54. — Wing of a pupa of Corydalis.

Accessory veins added proximally. — A good illustration of the adding of accessory veins to the proximal end of a series is afforded by the accessories of vein Cu_1 in the Blattidæ. Fig. 56 represents the hind wing of a nymph of a cockroach. An examination of the set of accessory veins borne by vein *Cu*1 shows that the distal members of the series are well developed, and that the growth of additional veins is taking place in the disk of the wing at the proximal end of the series. In this case the first accessory vein is the distal one.

Accessory veins interpolated. — In the wing of the cockroach represented by Fig. 56 there are many accessory veins borne on the cephalic side of radius. From the presence of the fine twigs near the apex of the wing, it is evident that accessory veins are being added distally. It is also evident that the number of veins is being increased by the splitting of certain of the older veins, *i.e.*, by interpolation. In cases of this kind it is impracticable to number the members of a series of accessory veins.

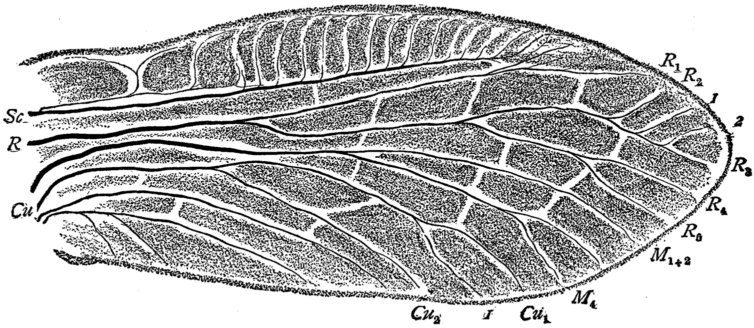

FIG. 55. — Wing of a pupa of Sialis.

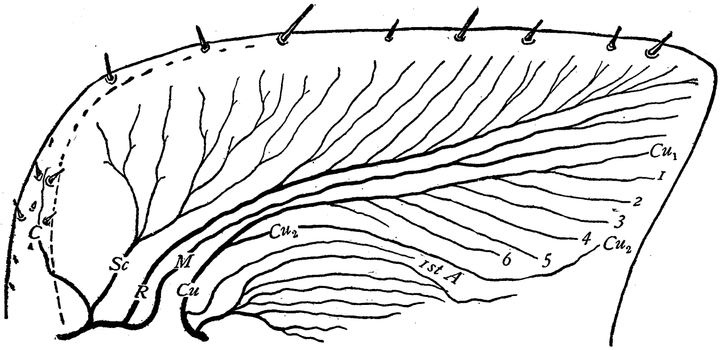

FIG. 56. — Hind wing of a nymph of a cockroach.

II. THE SUPPRESSION OF THE DICHOTOMOUS BRANCHING OF VEINS.

In the more highly specialized of the many-veined insect wings there exists a type of branching which is very different from that of our hypothetical primitive type. An examination of Fig. 57, which represents this type, will show that in every case the forked veins are branched dichotomously, while in the many-veined wings the more characteristic type of branching results in the formation of pectinate veins; this pectinate type of branching is well shown by the radial sector of Corydalis (Fig. 54).

The prevalence of the pectinate type of branching in the many-veined wings has been, doubtless, the greatest obstacle to a recognition of the homologies of the branches of the forked veins in such wings. Our hypothetical type was first worked out by a study of the few-veined wings; but it was a long time after that was accomplished before we saw that the pectinate type of branching had been derived from the same type. The most potent factor in reaching this conclusion was the fact that in some of the many-veined insects the dichotomous type of branching has been preserved. Good illustrations of this can be seen in the neuropterous genus Sialis (Fig. 55), while equally good examples of the pectinate type are presented by the closely allied genera Chauliodes and Corydalis (Figs. 53, 54).

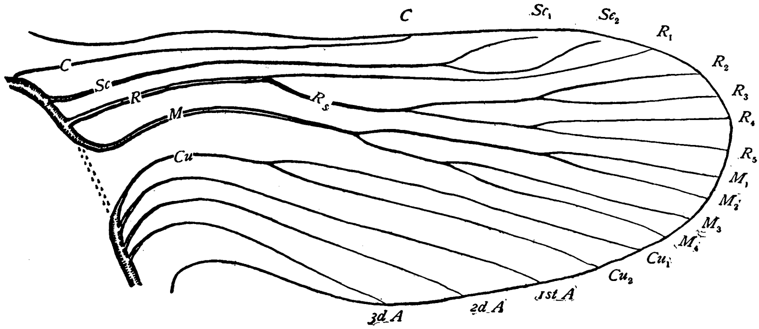

FIG. 57. — Hypothetical type.

The changes that take place in the development of the pectinate type of venation from the dichotomous type are of two kinds: first, the development of accessory veins; second, the modification of the primitive veins so that they are no longer dichotomously branched. The former has been discussed above; we will now briefly refer to the latter. For this purpose we will give a series of diagrams illustrating several types of branching of the radial sector.

Fig. 58*a* represents the typical or dichotomously branched radial sector. Fig. 58*b* represents a typical radial sector with the addition of some accessory veins on the caudal side of vein R_2. Such a radial sector occurs in the fore wing of Ithone.[1] In this case the radial sector is nearly pectinate, but not quite so, owing to the forked condition of vein R_{4+5}. In Chauliodes (Figs. 53, 58*c*) veins R_4 and R_5 coalesce to the margin of the wing; and in this way the pectinate type is attained. In Hemerobius (Figs. 58*d*, 59) the pectinate type has been attained by fission instead of coalescence. Here veins R_4 and R_5 have split apart till vein R_5 arises from the main stem of radius.

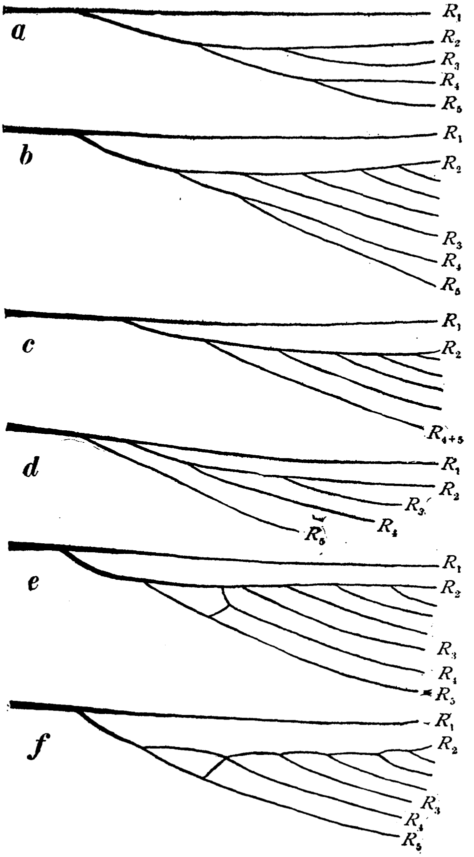

Fig. 58. — Diagrams of several types of radius.

When many cross-veins are present, the dichotomy of the branching of the sector may be suppressed in still another way, by the transference of the base of vein R_4 to vein R_{2+3}. All stages of this switching of vein R_4 occur in the Myrmeleonidæ; but two examples will suffice to illustrate it. In Myrmeleon (Fig. 58*e*) the base of vein R_4 appears to be forked; one arm of the fork arising from vein R_5, the other from vein R_{2+3}. The former is the true base of vein R_4; the latter is a cross-vein which is assuming the function of a base of this vein. In the hind wing of *Ptynx appendiculatus* (Fig. 58*f*) the switching has been completed, vein R_4 arising from vein R_{2+3}.

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[1] Brongniart. *Rech. sur l'Hist. d. Insectes Fossiles,* Pl. I, Fig. 10.

In the foregoing illustrations comparisons of allied insects have been made in order to determine the ways in which the wings are being modified ; frequently a comparative study of the fore and hind wings of a single insect is equally suggestive, for it often happens that the two pairs of wings exhibit different degrees of the same kind of modification, and thus the course of the change is indicated.

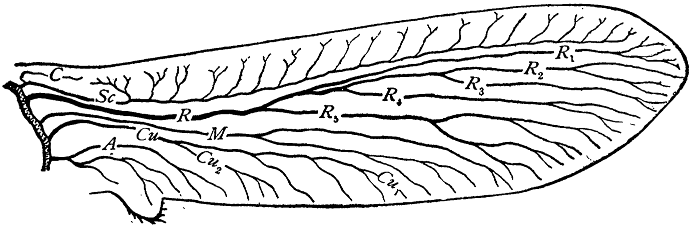

FIG. 59. — Wing of a pupa of Hemerobius.

A study of the causes of the changes which we are describing is beyond our present purpose, which is merely to determine the homologies of the wing-veins. But we can gain a hint of the probable reason for the development of the pectinate type of veins without entering very deeply into questions of the mechanics of flight.

It is obvious that many styles of flight exist among insects, and that for the different styles of flight different kinds of wings are required. In Corydalis (Fig. 54) the wing is stiffened, along a line parallel with the costal margin of the wing, by the subcosta, the main stem of the radius, and veins R_1 and R_2. Back of this line there is a broad, flexible area, which bends up during the downward stroke of the wing, forming an inclined plane, the pressure of which against the air forces the insect ahead. The flexibility of this area of the wing is increased by those changes which result in the formation of the pectinate type of branching.

The extreme of the pectinate type of branching exists in the neuropterous genus Polystœchotes, in which the area traversed by the parallel veins is very broad.